

ILLUMINATION, ANOTHER FUNCTION OF FIREFLY FLASHES?

JAMES E. LLOYD¹

ABSTRACT

*Photuris*² fireflies commonly emit characteristic flashes when landing and taking flight that appear to function in illumination. The landing flashes of males may provide clues to the origin of certain mating signals.

A perusal of the recorded observations and experiments of biologists who have been interested in the natural history of fireflies will reveal that firefly flashes function in mate identification and location (Harvey, 1952; Barber, 1951; Lloyd, 1966), the attraction of prey (Lloyd, 1965), the attraction of females to suitable oviposition sites (Kaufmann, 1965), and perhaps the intimidation of potential predators (Harvey, *ibid.*). It now appears that the function of certain flashes of *Photuris* is simply illumination.

The most frequently seen flashes of fireflies are the bright and distinctive advertising signals of flying males. *Photuris* fireflies, however, are commonly seen emitting dim flashes during flight, bright flickers when on the ground, and combinations of flickers and bright pulses when flying just above the ground and alighting. The last mentioned appear to be landing flashes that by illuminating the ground or vegetation beneath the insects aid in the location of suitable landing sites. Such illumination would have considerable adaptive value since there are a variety of hazards (e.g., spider webs and water puddles) when landing. In addition, since fireflies deposit their eggs on or near the surface of damp soil, the amount or nature of reflected light might provide females with important information on soil conditions.

I have observed the landing behavior of one species of Florida *Photuris* extensively and recorded its landing flashes. Females that are about to land will first be noted flying at altitudes between one and two meters and emitting dim, short flashes at 1–2 second intervals. They then fly toward the ground at a slight angle, increase their rate of flashing until their flashes fuse into a continuous flickering emission, and alight (Fig. 1). Low altitude passes are frequently made at several points before actual landing, and during this flight, flash rate increases and decreases inversely with altitude. The substrate beneath landing individuals is sufficiently illuminated to permit me to discern its vegetative nature. Once I observed a female descending over standing water on a lawn. At an altitude

¹ University of Florida.

² Coleoptera, Lampyridae.

of about 10 cm she flew up sharply and landed a few meters beyond in grass. Landing females usually land on prominent spikes or blades of grass. On oscillograms of recorded landing flashes the time of landing is usually obvious since immediately following a fusion of pulses (Fig. 1, f) light intensity sharply increases (Fig. 1, s). This sharp spike occurs when the female's light organ is suddenly no longer directed toward the ground but instead is better exposed to the recording equipment. After alighting, a few short flashes are emitted and then flashing ceases.

Males of this species can occasionally be seen landing. Their landing flash is a ragged flicker of discrete pulses, each of which is similar in duration to advertisement flashes of this species. Landing males of species with complex advertising flashes (e.g., Fig. 2) rapidly repeat what appear to be abortive or abbreviated advertisements when alighting.

Flickers are emitted by walking individuals, both males and females, of several species. Although some females appear to be ovipositing, others are walking or climbing through tangles of vegetation. The latter eventually take flight, emitting either a continuous, flickering flash or a rapid series of pulses as they fly upward through the vegetation, and then cease flashing as they turn and fly horizontally. Predaceous females of the *Photuris versicolor* group commonly emit series of pulses as they prepare to leave hunting perches. Such flashing almost always ends shortly after take-off.

Since males do not approach and flash near females that have recently landed and I have not observed characteristic differences in the landing flashes of various species I doubt that the female landing flashes have any function in sexual communication. I have not been able, with artificial, male mating flashes, to elicit flash responses from females that I have observed landing. These females have already mated since when brought into the laboratory many lay fertile eggs (Minnick and Lloyd, in prep.). If females that employ landing lights are not sexually responsive it is understandable why males are not attracted to them. In addition, since predaceous females flash in this context, natural selection may be rigorously removing males that approach such lights.

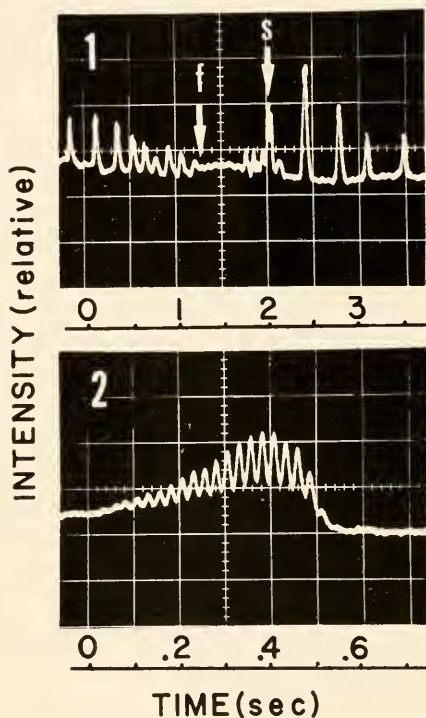
DISCUSSION

If these flashes of *Photuris* function in illumination as they seem to, they are analogous to the echo-location cries of bats; animals that are also nocturnal. In both systems the "echoes" of signals emitted by the animals provide them with information on the nature of their environment.

A knowledge of the male landing flashes of *Photuris* and its relatives could be useful in elucidating the evolution of mating signals. Since *Pho-*

turis males sometimes flash when landing near females that have answered their advertising flash, similar flashes in males of ancestral species may have become incorporated into mating signal sequences; that is, structurally distinctive advertising and courtship signals may have become essential preliminaries to mating. Such signal combinations could provide a source of species-specific advertising flashes during (or subsequent to) speciation. In this regard it is interesting that the advertising signals of at least four species of Nearctic *Photuris* are flickers of various frequencies.

Oscillograms of firefly flashes. Flashes are detected by a photo-multiplier tube, transduced to a frequency modulated audio signal that varies proportionally (9–12 kc) with light intensity, and recorded on magnetic tape (7.5 ips). For analysis, recorded tones are transduced to a variable dc voltage that is then fed into a storage oscilloscope with a calibrated time-base. The recording system was designed and built by Alton Electronics, Gainesville, Florida. FIG. 1. Landing flashes of *Photuris* species "A" female. Arrow f, flashes begin to be fused into a continuous, flickering emission. Arrow s, flash emitted immediately upon landing when female's light organ is no longer pointed at the ground. FIG. 2. Advertising flash of *Photuris* species "D" male; a 40 cps flicker superimposed upon a continuous emission.



ACKNOWLEDGMENTS

This investigation was supported by NAS Bache Fund, grant No. 500, and NSF grant No. GB-7407. I thank Thomas J. Walker of the University of Florida for his valuable comments and criticisms during the preparation of the manuscript.

LITERATURE CITED

- BARBER, H. S. 1951. North American fireflies of the genus *Photuris*. Smithsonian Inst. Collections, 117: 58.
 HARVEY, E. N. 1952. Bioluminescence. Academic Press, New York. 649 pp.

- KAUFMANN, T. 1965. Ecological and biological studies on the west African firefly *Luciola discicollis* (Coleoptera: Lampyridae). Ann. Ent. Soc. America, 58: 414-426.
- LLOYD, J. E. 1965. Aggressive mimicry in *Photuris*; firefly femmes fatales. Science, 149(3684): 653-654.
- LLOYD, J. E. 1966. Studies on the flash communication system in *Photinus* fireflies. Univ. Mich. Museum Zool. Misc. Pub. 130, 95 pp.

The Balance of Nature.—On and off for the past six years I have been guest siphonapterist at the Malaria Institute at Amani, Tanzania, East Africa. Amani is at 3,000 feet in the Eastern Usambara mountains. The Institute maintains several field stations in Tanzania, the largest being 20 miles down the mountain at Muheza, the elevation here being 500 feet, the location 25 miles inland from Tanga which is on the Indian Ocean.

Once a month I would come down to Muheza to trap low elevation mice to see if I could secure their fleas but I found them carrying none which seemed to uphold the siphonapteran saying that in East Africa, at least, native mice of the low elevations carry few, if any, fleas.

About 10 feet from the front door of the Muheza main rest house stood a small termite castle which was about 2 feet in height and in diameter. There was an irregular 6 inch flue in the center. The termites were small, perhaps $\frac{1}{8}$ th inch long and even the soldiers looked unimpressive. Hundreds of them worked the top of the castle keeping the lawn cropped down to the soil probably using the grass clippings for food. When the sun was just overhead one could look down into the flue and see comb not too unlike empty honey comb. This formation could be seen all over the mountains where roads had been cut into banks but when exposed the masses were deserted. The combs were slightly waxy and seemed to be of fine sand grains.

About 8 feet away from the termite castle stood a fair sized Mango tree. In it were colonies of those true ants which pull the leaves together and tie them into a bag. These ants were about $\frac{1}{2}$ inch long. Through the years a perfect balance had been maintained between the termites and the ants for from the base of the tree to the top of the termite castle a path one inch deep and wide was the highway of communication. The ants in a steady stream ran empty handed to the castle, captured a non-resisting termite, then back to and up the tree with a wiggling, dying termite, food apparently for the colony. This process was watched for four years. There never seemed too few termites or too many ants. Nature was balanced.

One day during the fourth year it was decided to see what was in the comb within the castle. The flue was slightly enlarged with a mallet, the comb grasped and cut away and taken up to Amani for study. The comb was found to be a fungus garden. All along the walls were large yeast-like budding basidiomycetes, white, opaque and about the size of pinheads. For only a short time did the nurse termites within the comb survive.

On the next visit to Muheza it was found that the grass on the castle top was two inches high, the termites were gone, of the ant highway there was not a trace and there were no ants in the Mango tree. The balance of nature had been broken. Both insects, deprived of their natural food had perished.—C. ANDRESEN HUBBARD, *Tigard, Oregon 97223*.